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The diet of Risso's dolphin, *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa

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Abstract

Examined the stomach contents of Risso's dolphins (*Grampus griseus*), stranded along the east coast of South Africa over a 22 year period (1969–1991). Prey consisted exclusively of cephalopods from which seventeen species were identified. Index of relative importance values were used to identify the most important prey. The most dominant prey *Loligo vulgaris reynaudii*, a shallow water, semi-pelagic subspecies constituted 81 % by mass of the total prey and 48.1 % and 29.2 % by number and frequency of occurrence, respectively. Other important species, were *Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* and *Ancistrocheirus lesueuri*. The diversity of prey species differed for males and females and also between dolphin size classes. These data suggest a partitioning of food resources between sub-groups. The results of this study indicate that Risso's dolphins probably feed in the Agulhas current and also in coastal waters where the continental shelf is narrow.

Introduction

The diets of cetaceans are determined to a large extent by their geographical location, as well as the seasonal and topographical changes in the abundance of their prey (Clarke 1986a). Risso's dolphins, *Grampus griseus*, are widespread in warm tropical and temperate pelagic (> 1000 m) waters (Aguayo 1975; Jennings 1982; Ross 1984). They are also frequently sighted at the continental shelf edge (Leatherwood et al. 1982; Ross 1984) and in coastal waters where the shelf is narrow.

Risso's dolphins feed almost exclusively on cephalopods (Tomilin 1957; Tsutsumi et al. 1961; Orr 1966; Stroud 1968; Mitchell 1975; Leatherwood et al. 1982; Ross 1984; Clarke and Pascoe 1985; Sekiguchi et al. 1992). Though the specific or generic identity of the prey species and their relative importance in the diet is not generally known. A knowledge of the prey preferences and the relationship of the diet to the social structure and movements of Risso's dolphins provides a better understanding of their biology.

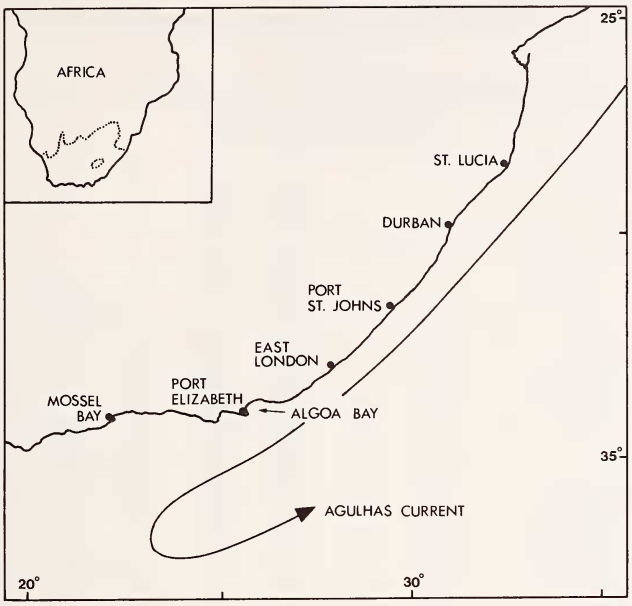
The aim of this study was to assess quantitatively the diet of Risso's dolphins stranded on the east coast of southern Africa, between Mossel Bay (34 °S, 22 °E), and St Lucia, Natal (28° 30′ S, 32° 30′ E) (Figure).

Material and methods

This study examined the stomach contents of 65 Risso's dolphins stranded between 1969 and 1991, and includes a re-examination of seven stomachs reported by Ross (1984). Stomachs were excised and washed in water until all loose tissue was removed and sorted (sensu Cockcroft and Ross 1990). Loose cephalopod beaks were stored in 10 % buffered formalin for later identification. Data recorded from strandings included date and locality of stranding, length and mass and sex of individuals.

Identification of prey remains used the Port Elizabeth Museum's reference collection of some 1,600 beaks of almost 300 cephalopod species. For each species, regressions relating beak dimension to prey weight and length are available. Cephalopod classification follows that of Clarke (1986b).

Beaks of all cephalopod species, except octopods and sepiids, were measured across the lower rostral length (LRL), to the nearest 0.05 mm, using Vernier calipers. The hood length (HL) was



The south-east coast of South Africa (see text for definition). The Agulhas current is a major oceanographic feature of the area and its flow follows the continental shelf edge

measured in the case of octopods and sepiids. Mantle length and reconstituted prey mass were then calculated from the beak measurements, using the appropriate regressions from the reference collection.

The minimum number of individuals of any cephalopod species in a stomach was assumed to be the greater number of either upper or lower beaks. Where upper beak numbers were larger, the length and mass of prey were determined from estimated lower beak dimensions.

The reconstituted mass of prey species within stomachs was determined from the established regressions. Where regressions were not available, reconstituted mass and length were extrapolated from available records. An index of relative importance (IRI) was calculated for each species according to Pinkas et al. (1971), where: IRI = (% number + % reconstituted mass) × % frequency of occurrence.

Results

Thirty three of the 65 stomachs were completely empty and the remaining 32 contained only cephalopod remains, though statistical analyses were based on all stomachs. From a total of 1341 prey items, 17 distinct species were identified; ten to known specific level and seven to unidentified species within known genera (Tab. 1).

Based on calculated Index of Relative Importance (IRI) values, the five most important prey species in the diet were; *Loligo vulgaris reynaudii, Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* and *Ancistrocheirus lesueri* (Tab. 1). These species were also the five most important by reconstituted mass and together contributed almost 92 % of the total reconstituted mass of prey taken (Tab. 1). However, *L. v. reynaudii* and *L. diadema* were clearly the most important in terms of frequency of occurrence and total numbers (Tab. 1).

Although there were similarities in the prey consumed by males and females, there was a significant difference (Diversity Index Comparison, t-test: $t = 10.8$, $df = 1303$, $P < 0.05$) in the diversity of prey they consumed (Tab. 2). Four species consumed by females were not found in males (Tab. 2).

Table 1. **Prey of Risso's Dolphins off the south-east coast of South Africa and their contribution to the diet**

Based on their absolute number, frequency of occurrence *(f)*, *reconstituted* mass (recon. mass), mean prey length, percentage number, percentage mass, percentage frequency of occurrence and Index of Relative Importance (iri)

Species	No.	*f*	recon. mass (g)	mean length (mm)	% No.	% mass	% *f*	iri
Order Sepiida								
Sepia sp.	21	3	70	40	1.6	0.0	4.6	7
Order Teuthida								
Loligo v. reynaudii	644	19	272458	262	48.0	81.0	29.2	3770
Lycoteuthis diadema	390	16	16430	96	29.1	4.9	24.6	836
Ancistrocheirus lesueuri	16	7	7512	188	1.2	2.2	10.8	37
Octopoteuthis sp.	14	6	3134	162	1.0	0.9	9.2	18
Moroteuthis sp.	4	3	231	5	0.3	0.1	4.6	2
Histioteuthis sp.	2	2	995	150	0.1	0.3	3.1	1
Brachioteuthis sp.	34	4	215	67	2.5	0.1	6.2	16
Todarodes angolensis	14	2	4574	230	1.0	1.4	3.1	7
Chiroteuthis veranyi	26	7	987	110	1.9	0.3	10.8	24
Teuthowenia pellucida	22	4	1739	202	1.6	0.5	6.2	13
Megalocranchia sp.	6	1	714	323	0.4	0.2	1.5	1
Cranchia scabra	32	6	1383	115	2.4	0.4	9.2	26
Order Vampyromorpha								
Vampyroteuthis infernalis	9	4	461	48	0.7	0.1	6.2	5
Order Octopoda								
Opisthoteuthis sp.*	8	3	337	56	0.6	0.1	4.6	3
Octopus magnificus	19	6	16081	160	1.4	4.8	9.2	57
Argonauta nodosa	80	8	9223	81	6.0	2.7	12.3	107
Total	1341		336550	135				

* No regressions available, length and mass estimated.

The largest cephalopod consumed was estimated at almost 400 mm (*O. magnificus*) and the smallest at 5 mm (*Sepia* sp.), although the calculated lengths of most prey fell between 100 and 200 mm, with a mean of approximately 140 mm (Tab. 1). However, the mean length of the dominant prey item (*L. v. reynaudii*) was greater and estimated at 262 mm (Tab. 1).

There was a poor correlation between dolphin length and both mean length of prey taken ($r = 0.26$) and the total reconstituted mass of prey consumed ($r = 0.28$). Generally, however, the maximum length of prey consumed increased with dolphin length and small cephalopod species (e.g. *Sepia* sp., mean length = 56 mm), which were important in the diet of smaller dolphins, were not taken by larger dolphins (Tab. 3). Similarly, larger cephalopod species, such as *Todarodes angolensis* (mean length = 230 mm) and *O. magnificus* (mean length = 160 mm) were important for larger dolphins, but were not taken by smaller dolphins. The mean length of the prey of males (208 mm) was significantly greater than that of females (146 mm) (Student's t-test: $t = 12.79$, $df = 1336$, $P < 0.05$). In contrast, there was no significant difference between the total mass of prey taken by individual males and females (Student's t-test: $t = 0.95$, $df = 30$, $P > 0.05$).

There was no significant difference between the diversity of prey items taken by large (> 250 cm) and small dolphins (< 250 cm) (Diversity Index Comparison, t-test: $t = -1.81$, $df = 881$, $P > 0.05$). Likewise, there was no significant difference between the mean length of prey taken by these two classes (Student's t-test: $t = 0.326$, $df = 24$, $P > 0.05$).

Table 2. **Index of Relative Importance (iri) and rank of importance of the prey taken by male and female Risso's dolphins**

Species	Males		Females	
	iri	rank	iri	rank
Order Sepiida				
Sepia sp.	1		20	
Order Teuthida				
Loligo v. reynaudii	4987	1	2633	1
Lycoteuthis diadema	687	2	1048	2
Ancistrocheirus lesueuri	32	6	55	7
Octopoteuthis sp.	4	9	52	8
Moroteuthis sp.	4	10	1	
Histioteuthis sp.			7	
Brachioteuthis sp.			67	6
Todarodes angolensis			38	10
Chiroteuthis veranyi	11	7	50	9
Teuthowenia pellucida	41	4	3	
Megalocranchia sp.			5	
Cranchia scabra	1		93	5
Order Vampyromorpha				
Vampyroteuthis infernalis	1		15	
Order Octopoda				
Opisthoteuthis sp.*	5	8	2	
Octopus magnificus	33	5	125	3
Argonauta nodosa	145	3	101	4
Number of stomachs	25		34	

* No regressions available, length and mass estimated.

The mean number of prey per stomach was 42 (range 1–282). There was little correlation ($r = 0.018$) between the mean number of prey per stomach and dolphin length. Additionally, there was no significant difference between the number of prey taken by males and females (Anova: $F = 0.255$, $df = 30$, $P > 0.05$).

In general, the prey variety in any stomach was low (mean of 3 species, range 1–9), with little correlation between the length of dolphin and the number of prey species taken ($r = 0.063$). Also, there was no significant difference between the number of prey species consumed by males and females (Anova: $F = 1.599$, $df = 30$, $P > 0.05$).

A total of nine stomachs were examined from animals stranded in summer (October–March) and 25 from those stranded in winter (April–September). Despite these low numbers, there was a significant difference between the diversity of prey species taken in winter and summer (Diversity Index Comparison, t-test: $t = 18.83$, $df = 1204$, $P < 0.05$), with eight species taken in winter not consumed in summer (Tab. 4).

Discussion

The interpretation of cetacean diet based on analyses of the stomach contents of stranded individuals may be subject to a number of biases (Ross 1984; Clarke 1986a; Sekiguchi et al. 1992). Firstly, the apparent ill health of the majority of singly stranded cetaceans (Ross 1984) may result in either an empty stomach, or the stomach containing only a few typical prey items eaten prior to the illness. Secondly, the dietary importance of cephalopods is easily overestimated, because their hard remains (beaks) are retained and are identifiable

Table 3. **Index of Relative Importance (iri) values, rank of importance and mean length of the prey taken by large (>250 cm) and small (<250 cm) Risso's dolphins**

Species	Dolphin length >250 cm			Dolphin length <250 cm		
	iri	rank	mean length (mm)	iri	rank	mean length (mm)
Order Sepiida						
Sepia sp.				167	6	56
Order Teuthida						
Loligo v. reynaudii	8215	1	262	3030	2	255
Lycoteuthis diadema	543	2	99	7243	1	98
Ancistrocheirus lesueuri	47	5	173	257	4	208
Octopoteuthis sp.	12	11	174		5	147
Moroteuthis sp.	6	13	5	20		
Histioteuthis sp.	1	15	137	137	11	162
Brachioteuthis sp.	8	12	65		8	77
Todarodes angolensis	26	7	230	144		
Chiroteuthis veranyi	25	8	119	28	7	103
Teuthowenia pellucida	28	6	204	37		196
Megalocranchia sp.				275	9	323
Cranchia scabra	12	10	120		3	114
Order Vampyromorpha						
Vampyroteuthis infernalis	19	9	48			
Order Octopoda						
Opisthoteuthis sp.*	6	14	82	8	12	42
Octopus magnificus	192	4	160			
Argonauta nodosa	286	3	81	36	10	79
Number of stomachs		24			9	

* No regressions available, length and mass estimated.

for longer periods than fish otoliths (Clarke and MacLeod 1982; Bigg and Perez 1985; Clarke 1986a). For pelagic animals, both these sources of bias may be compounded by the remains of prey consumed during the animal's transit of inshore waters before beaching (Ross 1984; Clarke 1986a).

At least two studies have attempted to quantify any biases inherent in dietary studies from stranded cetaceans. In a comparison of the diet of non-stranded and stranded animals, Sekiguchi et al. (1992) demonstrated that the latter were biased, but a similar analysis by Ross (1984) showed no such bias. In view of the contradictory nature of these two studies, interpretations from the present study are assumed to reflect the diet of Risso's dolphins from the east coast of South Africa.

Like the study of Ross (1984), this study indicates that Risso's dolphins off the south-east coast of South Africa feed exclusively on cephalopods. Although Risso's dolphins consume at least 17 species, their diet is dominated by the 'chokker' squid, *L. v. reynaudii*, a fairly common cephalopod inhabiting the south-east coast of South Africa (Augustyn 1990). Based on calculated IRI values and reconstituted weights of stomach contents, four other cephalopods were also important in the diet (*A. lesueuri, A. nodosa, L. diadema,* and *O. magnificus*). Though there was some small variation in the relative importance of these five major prey, their continued presence throughout the study and for all size and sex classes of dolphins, is significant and may reflect their relative availability in this region.

Exclusive cephalopod diets are also recorded for Risso's dolphins stranded or captured in British waters (Tomlin 1957), the Mediterranean (Pilleri and Gihr 1969), Japanese waters (Tsutsumi et al. 1961) and the eastern Pacific (Orr 1966; Stroud 1968). Addition-

Table 4. **The relative importance (percentage mass, number and frequency) (*f*) of occurrence and Index of Relative Importance (iri) of the prey of Risso's dolphins taken in winter (April–September) and summer (October–March)**

Species	Winter				Summer			
	% mass	% No.	% *f*	iri	% mass	% No.	% *f*	iri
Order Sepiida								
Sepia sp.	0.1	2.6	6.8	18				
Order Teuthida								
Loligo v. reynaudii	60.0	21.9	31.8	2606	89.3	31.6	93.4	5570
Lycoteuthis diadema	12.8	46.8	34.1	2032	0.9	5.3	0.0	5
Ancistrocheirus lesueuri	2.8	1.3	11.4	47	0.9	10.5	1.8	29
Octopoteuthis sp.	2.3	1.5	11.4	43	0.4	5.3	0.1	2
Moroteuthis sp.	0.2	0.5	6.8	5				
Histioteuthis sp.	0.8	0.2	4.5	5				
Brachioteuthis sp.	0.2	4.1	9.1	39				
Todarodes angolensis	3.6	1.7	4.5	24				
Chiroteuthis veranyi	0.8	3.0	13.6	52	0.2	5.3	0.0	1
Teuthowenia pellucida	1.0	1.9	9.1	27	1.1	5.3	0.2	7
Megalocranchia sp.	0.6	0.7	2.3	3				
Cranchia scabra	1.1	3.9	13.6	68				
Order Vampyromorpha								
Vampyroteuthis infernalis	0.4	1.1	9.1	13	0.2	5.3	0.0	1
Order Octopoda								
Opisthoteuthis sp.*	0.3	1.0	6.8	8				
Octopus magnificus	8.1	0.7	6.8	60	2.6	21.1	3.2	124
Argonauta nodosa	5.2	6.9	15.9	193	4.3	5.3	1.2	29
Number of stomachs				44				19

* No regressions available, length and mass estimated.

ally, Risso's dolphins in captivity accept only squid (Tsutsumi et al. 1961). Other than two fish species found in the stomachs of Risso's dolphins stranded off South Africa (Sekiguchi et al. 1992), no fish remains have been found in this species. These data infer that Risso's dolphins consume a small variety of locally abundant cephalopod prey and that it is inappropriate to consider this species an opportunistic predator. This is not unusual, some cetaceans are relatively restricted in their diet, regularly feeding on only a few types of prey (Fiscus 1982).

Though most of the cephalopod prey taken by Risso's dolphins are oceanic, benthic neritic and mid-water neritic species are also consumed (Roper et al. 1984; Clarke 1986a; Clarke 1986b). These data indicate that Risso's dolphins feed not only in the epi- and meso-pelagic zones of the ocean, but also over the continental slope and shelf areas. However, the dominant prey species (*L. v. reynaudii*) is neritic, inferring that Risso's dolphins feed primarily over the continental shelf. Although this conclusion may be influenced by the biases discussed earlier, Risso's dolphins are sighted most frequently along the continental shelf edge and are often seen in coastal waters where the shelf is narrow (Leatherwood et al. 1982; Ross 1984). Additionally, Risso's dolphin distribution is probably related to the movements of their prey, as is that of other pelagic dolphins (Norris and Dohl 1980). In combination, these data suggest that the present results reflect the normal diet of Risso's dolphins for the south-east coast of South Africa.

Most of the cephalopod species eaten by Risso's dolphins are ammoniacal, buoyant, solitary species, evenly and widely distributed, while the remainder are muscular, fast

swimmers, occurring in large aggregations (Clarke 1986a). Dolphins which occur in small groups, like Risso's dolphins, are known to prey on species with the former characteristics (Ross 1984) and this may explain the great variety of ammoniacal squid eaten. The latter characteristics are typical of *L. v. reynaudii* and almost certainly account for this species' high frequency of occurrence and abundance in individual stomachs. It is interesting that 70 % of all Risso's dolphin prey, both oceanic and neritic, are luminous or have photophores (Clarke 1986a), possibly making their capture easier.

Male and female Risso's dolphins take different prey sizes and although there was no clear relationship between dolphin and prey size, larger dolphins consumed larger cephalopod prey than smaller dolphins. Though the latter may only be a result of the physical limitations of the smaller mouths of small dolphins, these data in combination, indicate some form of sex, and perhaps size, related partitioning of available resources. Risso's dolphins generally occur in small groups that are often part of a larger, widespread aggregation (Ross 1984). Although the size and sex structure of these groups is unknown, it seems feasible that they may be sex or size based to alleviate competition for resources. Such sex and size group partitioning is evident in bottlenose, and perhaps other dolphins, where sub-groups exploit different foraging ranges, prey sizes and species, to reduce intraspecific competition (Cockcroft and Ross 1990).

The reasons for the seasonal variation in the prey spectra of Risso's dolphins is unknown. Although this may be an artifact of the differing seasonal frequency of strandings, it may also reflect seasonal changes in the availability of the prey, especially the summer abundance of *L. v. reynaudii* (Roper et al. 1984).

The fishery for *L. v. reynaudii* is the most important commercial fishery off the south-east coast of South Africa (Augustyn 1990) and it is expanding rapidly. This cephalopod is also an important and primary food resource for Risso's dolphins and other marine mammals (Ross 1984; Castley et al. 1991; Young 1993) off the south-east coast of South Africa. In view of the current level and envisioned expansion of the commercial fishery, there may be existing and potential competition for this resource between fisheries and marine mammals. Consequently, an assessment of the impact of marine mammals on cephalopod stocks and the determination of the extent and potential interactions between fisheries and marine mammals is important.

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Zusammenfassung

Die Nahrung von Risso's Delphinen, Grampus griseus (Cuvier, 1812) an der südafrikanischen Ostküste

Untersucht wurden die Mageninhalte von 65 gestrandeten Risso's Delphinen (*Grampus griseus*), die über einen Zeitraum von 22 Jahren (1969–1991) an der südafrikanischen Ostküste gesammelt worden waren. Ausschließlich Tintenfische, insgesamt 17 verschiedene Taxa, wurden anhand ihrer unverdaulichen Schnäbel als Beute identifiziert. *Loligo vulgaris reynaudii*, ein semi-pelagischer Tintenfisch aus dem Flachwasser des Kontinentalschelfes, dominierte die Nahrung mit 81 % Gewichtsanteil, machte 48.1 % aller gezählten Cephalopoden aus und erschien in 29.2 % aller Mägen mit Inhalt. *Lycoteuthis diadema, Argonauta nodosa, Octopus magnificus* und *Ancistrocheirus lesueuri*, sämtlich Arten, die am Schelfabhang vorkommen, waren die nächst wichtigsten Nahrungstiere. Die Artenzusammensetzung der Beute deutet daraufhin, daß Risso's Delphine ihre Nahrung im warmen Agulhas Strom über dem Schelfabhang finden, aber auch dort in Küstengewässern, wo der Kontinentalschelf schmal ist. Geschlechts- und größenspezifische Unterschiede in der Beutewahl wurden ermittelt. Diese Daten lassen vermuten, daß eine Aufteilung von Nahrungsresourcen zwischen sozialen Gruppen stattfindet.

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